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ABSTRACT

The Fjord horse originates from Norway but forms a global population due to several small populations in foreign countries. There exists no information about the additive relationship and the genetic variance between these subpopulations. By collecting blood samples from Norwegian and Swedish Fjord horses, a sample of 311 Norwegian and 102 Swedish horses gave 485,918 SNPs available for analysis. Their inbreeding coefficients were calculated and compared to the pairwise coancestry and the shared genomic segments. The effective population size was almost similar with the two methods in the Norwegian Fjord horse population (63 and 71), but very different in the Swedish population (269 and 1136) and unprecise due to a much smaller number of observations. The study showed that coancestry from shared genomic segments can be used to estimate additive genetic relationship and genetic variation within and between the global populations of the Fjord horse.

Introduction

The Norwegian Fjord Horse has its origin in the Western part of Norway, where it traditionally was used for amongst others agricultural and conveyance purposes in the steep, inaccessible fjord and mountain areas. In the middle of the nineteenth century, the Fjord horse was a part of the first governmental initiative on horse breeding. It was established a stud farm on Hjerkinn, which a decade later was phased out due to poor management (Dahle, 2006). Instead, as a governmental initiative to improve the breed, Norwegian Døle stallions were crossed into the breed. Due to high-tempered discussions about the effect of the crossbreeding, this effort lasted relatively short. From the early years of the twentieth century, there was a common understanding of the use of pure breeding in the Norwegian Fjord horse (Nestaas, 2010). The first studbook on the Fjord horse was published in 1910, including horses born as early as 1857 (Nestaas, 2010). The number of horses in Norway, and thus the number of Fjord horses, was reported frequently until the first half of the twentieth century. In 1921, there were 876 mated mares, which was a decline of 64% in three years (Nestaas, 2010).

After the first world war, there was a post-war crisis in Norway, but during the 1930s the situation gradually improved, which also was reflected in the number of horses. In 1930, as many as 1,893 Fjord mares were mated, and the total number of horses turned 200,000 in Norway within the end of that decade (Nestaas, 2010).

In the last decades, the Fjord horse and its areas of use have changed from work to sports and leisure purposes, also facing strong competition from imported, specialized horse breeds in these latter market segments. The greatest challenge for the modern Fjord horse is to improve the competitive edge and develop according to the demand in the market. This might increase the population size, which is essential to maintaining and developing the genetic resource represented by the breed. Since the Norwegian population of the Fjord horse only consists of about 5000 animals, with less than 150 foals born per year (Furre, 2016), this requires surveillance and management of the genetic variation to ensure an *in vivo* population of this national breed in the future.

There are Fjord horse populations in several countries, and the global population size is far larger than the Norwegian one. There is limited formalized cooperation

between the breeding associations in the different countries, and there is no overall genetic management of the global Fjord horse population. Fjord Horse International (FHI) is an international forum where member countries can exchange information about breeding, sport and education regarding the purebred Fjord horse worldwide (FHI, 2017). Today, the FHI has 13 member countries, and Norway is regarded as the country of origin of the Fjord horse, giving a certain demand for Fjord horses from Norway. The Norwegian import of Fjord horses is quite limited, but there have been some imports, mainly from Denmark and Belgium. One role of the FHI is to develop future breeding of the Fjord horse in cooperation between these countries. Norway has, as the country of origin for this breed, a responsibility to initiate and coordinate such a process. For comparison, the Agricultural Society of Iceland established already in 1990 the database Fengur for recording of all data in horse breeding for the Icelandic horse (Hugason, 1994), later to become WorldFengur (https://www.worldfengur.com/), which is a global studbook for this breed.

To improve the international breeding collaboration, there is a need to develop methods for calculating the additive relationship and the genetic variance within and between populations without having any pedigree data available. It is well known that using pedigree information for calculating the relationship across populations can be extremely demanding and even unreliable, as an individual does not have a unique identity across populations due to different systems for identifying individuals in the different countries. However, the use of genetic markers makes it possible to gain information about the individual relationships within and between populations, independently of the pedigree information available. Several studies have reported consistency between genealogical and genomic relationships (e.g. Li et al., 2011; Saura et al., 2013; Mastrangelo et al., 2014; Rodríguez-Ramilo et al., 2015), indicating that genomic data is a useful tool in the case of complex or absent genealogical information. The use of runs of homozygosity (ROH), which are long stretches of DNA segments, for calculating individual inbreeding has been studied in several horse populations (Khansour 2013; Metzger et al., 2015; Kamiński et al., 2017; Druml et al., 2017). Even if the use of ROH is more widespread (Peripolli et al., 2017), various molecular coancestry methods have been studied within commercial livestock breeds, although not in horses. When concerning the genetic diversity, the use of coancestry can maintain genetic variation and is used for instance in optimal contribution selection (Meuwissen, 1997; Sonesson & Meuwissen, 2001). Recently, molecular methods have been developed for the purpose of calculating the coancestry, replacing

pedigree data (e.g. Cara et al., 2011; Gómez-Romano et al., 2013; Clark et al., 2013; Toro et al., 2014). Also, as SNP-by-SNP coancestry does not discriminate deleterious mutations leading to lowered fitness, methods based on shared genomic segments have been suggested (Cara et al., 2013; Bosse et al., 2015, Rodríguez-Ramilo et al., 2015; Gómez-Romano et al., 2016). The method implies calculating the fraction of shared genomic segments, and to maintain the genetic diversity one aims to decrease the numbers and the length of the shared segments. Together with selection for optimal contributions, segment-based coancestry (SBC) has been shown to reduce the loss of fitness (Bosse et al., 2015).

The Swedish Fjord horse population was established with imports of Norwegian Fjord horses, and the organized breeding was initiated during the 1950s (Kättström, 2019). Still today, this population is bred according to the Norwegian breed standard, and in 2017 there was born 75 foals in Sweden (Kättström, pers. comm.). There are less than 150 Swedish breeding mares, but the total population size is not known. The small population size and the close collaboration that is possible between neighbouring countries made the Swedish population a natural choice in order to evaluate methods to assess the genomic relationship.

The aim of this paper was to estimate the additive relationship and the genetic variation within and between the Norwegian and the Swedish Fjord horse populations and to compare methods utilizing information from pedigree and shared homozygote segments.

Material and methods

A pedigree file with 26,462 individuals born in the period 1857–2015, containing all registered Norwegian Fjord horses in the period, was used. Of these, 206 individuals had originally been registered abroad, of which 63% were from Denmark. Others were from either Sweden (15%), Germany (15%), the Netherlands (6%) or others (1%). Some of these horses appeared in the studbook because they are themselves re-registered in Norway or have got progeny in Norway. Then, 5 generations of pedigree information are recorded, if available. The original file was edited for obvious or logical errors, and individuals only occurring as parents were added with as individuals, resulting in a file of 25,364 individuals. Missing (< 0.5%) or erroneous birth years were reconstructed either by use of external information, if available, or by making fictive birth years. The fictive birth years were set to one year older than the eldest offspring of the individual. Finally, the individual inbreeding coefficients for the 25,364 individuals were calculated, by use of *proc inbreed* in SAS® version 9.4.

For the Swedish Fjord horses, a similar data file consisting of 14,595 registered animals was received from the Swedish Horse Breeding Society. Of these, 36% was originally registered in another country, with 17% from Norway and 13% from Denmark. Other countries represented were Germany, the Netherlands, Finland, Poland and Great Britain. A total of 27% of all registered individuals had unknown birth year information. Thus, there were not made any attempt to replace these missing values with fictive birth years or to calculate the average coefficient of inbreeding per year. Further, the file was used to trace pedigree information (by EVA), as described later.

Blood samples from 365 Norwegian and 103 Swedish Fjord horses were collected in the period December 2015 to March 2016. The sampling was done either by local veterinarians, who froze the samples and sent them to the university (NMBU) by mail, or by a team from the project, travelling around in the eastern part of Norway. Of these, 432 samples were genotyped (329 Norwegian and 103 Swedish samples). Due to two separate funding sources, the samples were analysed in two steps, separate in time: The first batch (336 samples) was genotyped during spring 2016, and the last batch (96 samples) was genotyped during winter 2017. Affymetrix' high-density Axiom™ Equine Genotyping Array was used for the genotyping, featuring 670,796 SNP markers. The SNP genotypes were called using the software Axiom Analysis Suite (v. 2.0.0.35). The subsequent analyses were performed at the merged dataset. A quality control (QC) was accomplished with two levels of filtering; (i) Dish QC (threshold 0.82), measuring a number of non-polymorphic loci for which a clear signal is expected (e.g. only A or only G) that is distinguishable from background signal, indicating, for example, low-quality DNA, and (ii) QC Call Rate (threshold 0.97), which calculates the per cent of genotypes assigned to a subset of SNPs, being robust, well-performing SNPs, defined in advance based on earlier genotyping studies. A total of 423 samples passed the quality control (202 males and 221 females), for which genotypes of 505,601 SNPs were assigned. Genotypes were loaded to PLINK 1.9 (Purcell et al., 2007) and exposed to a third filtering, where SNP markers were deleted due to the following criteria: (i) those deviating from Hardy-Weinberg equilibrium, indicating e.g. genotyping error ($p \leq 10^{-5}$), (ii) those with a high frequency of missing (GENO > 0.05) and (iii) those being on the sex chromosomes. Six horses were removed due to missing pedigree information, and four were removed because they were duplicates erroneously tested twice. This resulted in a total of 413 animals in the reference population (311 Norwegian and 102 Swedish; 198

males and 215 females) and 485,918 SNPs available for analysis.

By use of EVA (Berg et al., 2006), the pedigrees of the 311 Norwegian and the 102 Swedish Fjord horses were traced back to the founders. The Norwegian pedigree data was ordered by birth year, whereas the Swedish data was ordered by generation, due to their lacking information of birth years. A founder was defined as an animal with both parents unknown. Animals with only one parent missing were defined as a half-founder, with the unknown parent considered as an unknown founder (Boichard et al., 1997). The complete generation equivalent (CGE) was calculated as

$$CGE = \frac{1}{N} \sum_{j=1}^{N} \sum_{i=1}^{n_j} \frac{1}{2^{g_{ij}}},$$

where N is the number of individuals in the reference population, n_j is the number of ancestors generated for animal j and g_{ij} is the number of generations between individual j and its ancestor i (Boichard et al., 1997). CGE can be interpreted as the number of generations in a comparable complete pedigree, illustrating the depth of the pedigree data.

Individual inbreeding coefficients in the reference populations were calculated using the traced pedigree (F_{ped}) and EVA (Berg et al., 2006).

The pairwise coancestry of the reference animals was calculated based on either pedigree information (f_{ped}) or shared genomic segments (f_{seg}). For the coancestry calculations based on pedigree, all test animals within the country were paired to each other, giving 48,205 Norwegian animal pairs and 5,151 Swedish animal pairs. The R-Studio package Kinship2 (Sinnwell et al., 2014) was used for calculating f_{ped}, excluding selfing. The f_{seg} was calculated with an identity by descent (IBD) detection algorithm in BEAGLE 4.1 (Browning & Browning, 2013), in a two-step procedure giving 20,865 records from Norway, 2242 records from Sweden and 36,974 records from both countries. In such a procedure, the shared haplotypes are at first identified by the GERMLINE algorithm (Gusev et al., 2009), and secondly, evidence of IBD is assessed through a refinement of candidate segments with a probabilistic approach. The default settings were used except for the effective population size, being replaced by a previous estimate of 83 (obtained by us of pedigree for all 25,364 individuals and the log regression approach described below), and a LOD score value. The LOD score is the logarithm of the odds and is used to prune out shared segments that are not common in a population, meaning that the default value of 3 was considered too high for our purpose. To find most of the shared segments, the LOD score was

set to 0.1, which was the lowest acceptable value. Shared segments of length $\geq$ 100 kb were retained, and f_{seg} was then calculated according to Cara et al. (2013):

$$f_{seg(i,j)} = \frac{\sum_k \sum_{a_i=1}^{2} \sum_{b_j=1}^{2} (L_{seg_k}(a_i,\ b_j))}{4L_{auto}},$$

where $L_{seg_k}(a_i,\ b_j)$ is the length of the k-th shared IBD segment seg_k over the homologue a of individual i and homologue b of individual j, and L_{auto} is the length of the autosomal genome.

The relationship between Y (f_{seg}) and X (f_{ped}) can be estimated by use of Wright's F-statistics (Falconer & McKay, 1996) that can be expressed as:

$$(1-Y) = (1-X)(1-F_{pop}),$$

where F_{pop} is common to all individuals in the population. Further, using the natural logarithm to deal with the non-linearity of this expression gives:

$$\ln(1-Y) = \ln(1-X) + \ln(1-F_{pop}),$$

which leads forward to the following simple linear regression model that can be applied on an individual basis (i):

$$\ln(1-Y)_i = y_i = \beta_0 + \beta_1 \cdot \ln(1-X)_i + e_i,$$

where β_0 is a constant expected to equal $\ln(1-F_{pop})$, β_1 is the regression coefficient of expected heterozygosity (pedigree-based) on observed heterozygosity (SNP based), and e_i is the random error term.

To quantify the rate of genetic drift, the rate of inbreeding (ΔF) was calculated as:

$$\Delta F = (1 - e^{b_1 \pm 1.96 * s.e.})L,$$

where L is the estimated generation interval calculated as the average age of the parents when the selected offspring were born (Falconer & Mackay, 1996), utilizing the traced pedigree of the first batch of genotyped animals. Moreover, b_1 is the regression coefficient from a log regression of the birth year (Pérez-Enciso, 1995) on the response variables, y_i. These were either based on the individual inbreeding coefficients from the traced pedigree data, $\ln(1-F_{ped})_i$, or from coancestry, $\ln(1-f_{seg})_i$. In the calculation of $\ln(1-f_{seg})_i$, a compromise was made between the need of assigning a precise birth year to a 'progeny' and to include as many 'progeny' or coancestry elements as possible in order to reduce the standard error of the estimate. Pairs born in the same ten-year cohort were combined and the 'progeny' was given a pseudo birth year based on the average birth year of the pair. Finally, the two dependent variables were exposed to the following linear regression model:

$$y_i = b_0 + b_1 \cdot X_i + e_i,$$

where b_0 is an unknown constant, b_1 is the regression coefficient associated with the regressor X_i, the birth year of individual i, and e_i is a random error term.

The effective population size (N_e) and its confidence interval were calculated according to Falconer & Mackay (1996):

$$N_e = 1/2\Delta F$$

Results

The Fjord horse population in Norway has had a steady increase in the average inbreeding coefficient since the start of the studbook in 1857 (Figure 1). In the period after 1990, the rate of inbreeding flattens out giving an average inbreeding of around 7%. Also, in the same period after 1990, the annual number of registered foals in Norway has been dropping quite drastically to below 100. The steep increase in the number of animals around 1990 was due to a shift in registration rules opening for all born horses to become registered, otherwise the population has been slowly built up after the major change in the production of horses after World War 2. In the Swedish Fjord horse studbook, too many individuals lacked information of birth year to be able to calculate the average inbreeding coefficient per year in a reliable way or displaying the number of foals registered per year.

The birth years of the test animals contributing to genotyping data have a time span of 28 years in the Norwegian population and 31 years in the Swedish population (Figure 2). There is a natural decrease in the presence of the eldest birth years in both populations, and around 80% of the test animals are born in the period 1999–2016. However, with the exception of some of the earliest years, all years were present in the test material of both populations.

Due to practical and economic reasons regarding the collection of blood samples, there were over three times as many genotyped animals from the Norwegian population than from the Swedish (Table 1). Both populations had a complete generation equivalent as high as around 12, but the Norwegian population turned over generations faster, with a generation interval of 9.1 years, versus 11.6 years in Sweden (Table 1).

The inbreeding coefficients from the pedigree (F_{ped}) were most expressed in the Norwegian population, with a level of 7.7%, and with the highest occurrence of individual inbreeding coefficient of 19% (Table 2). Whereas the Swedish population had an average level of inbreeding from pedigree of 5.2%. The level of the coancestry
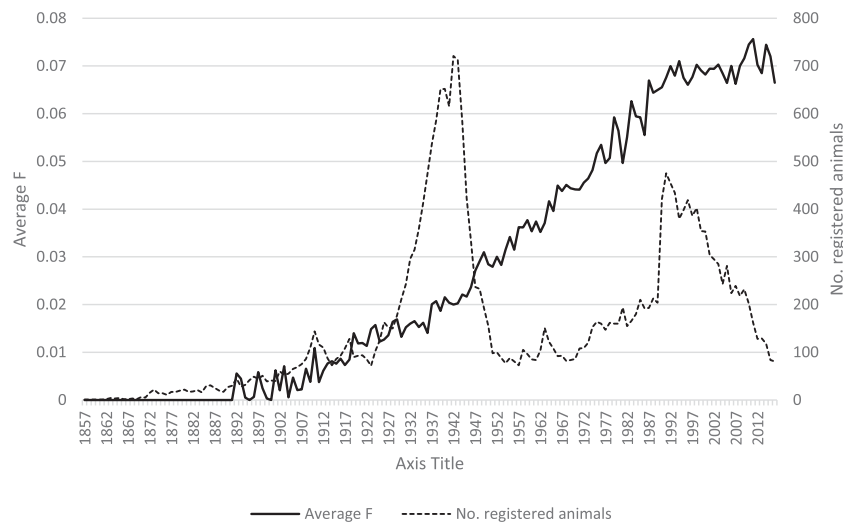
Figure 1. Average coefficient of inbreeding (F) per birth year and number of animals in the pedigree per birth year for the Norwegian Fjord horse population over the period 1857–2016.

coefficients from pedigree (f_{ped}) corresponded with the level for the inbreeding coefficient (Table 2). In both populations, the level of inbreeding from genomic coancestry (f_{seg}) was more than twice that from pedigree, and the average genomic coancestry coefficient between the Norwegian and Swedish populations was almost as large as within the Swedish population (Table 2). The relationship between the genomic and the pedigree-based coefficients is shown in Table 3. For the chosen segment length, the coancestry heterozygosity (f_{seg}) retrieved a regression coefficient close to 1 (NOR: 0.98; SWE: 0.95), and relatively high variability was explained by the model ($R^2 = 0.64$ and 0.82, respectively).

The rate of inbreeding from pedigree or coancestry from shared genomic segments was estimated as the slope in a log regression on birth year (Table 4). With both methods, the slopes were considerably steeper in the Norwegian population, leading to smaller effective population sizes. The effective population size from pedigree (F_{ped}) was 71 in the Norwegian population and 269 in the Swedish, whereas the effective population size from genomic coancestry (f_{seg}) was 63 in the Norwegian population and 1136 in the Swedish population (Table 4). For the genomic-based slope, the standard errors for the Swedish animals were larger than the Norwegian one, leading to a larger range of the confidence interval of the effective population size with an upper confidence limit including infinity (Table 4). Nevertheless, for both methods, the range of the confidence interval of the effective population sizes was lower in the Norwegian
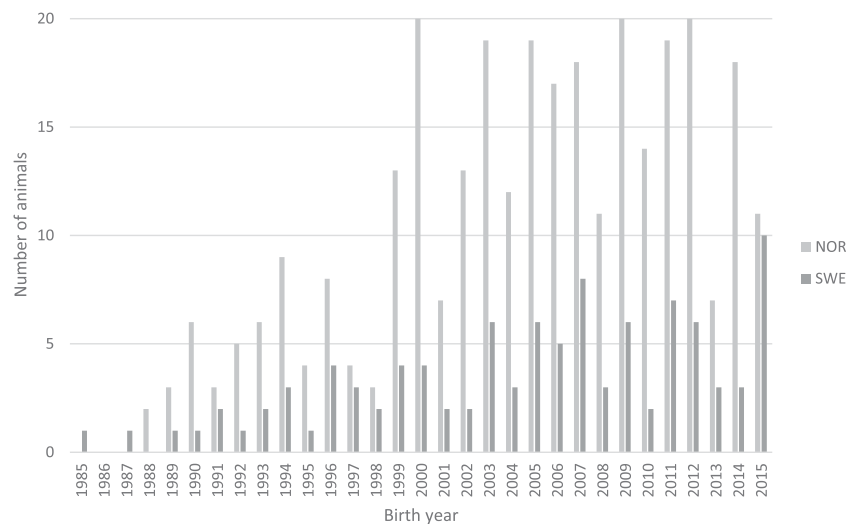
Figure 2. The age distribution of the animals contributing with genotype data (recorded December 2015 to March 2016), shown through the number of animals born per year in the Norwegian ($N = 311$) and the Swedish Fjord horse populations ($N = 102$).

Table 1. Number of Norwegian (NOR) and Swedish (SWE) individuals passing the genotype tests (reference population) and their estimated complete generation equivalent and generation interval per population.

	NOR	SWE
# animals in reference population	311	102
Complete generation equivalent (CGE)	12.7	11.6
Generation interval[a]	9.1	11.6

[a]Calculated from a subset of the genotyped horses (224 NOR and 103 SWE).

population than in the Swedish, and even more precisely estimated from pedigree than from shared genomic segments (Table 4). In the joint analysis of the two populations, the genetic coancestry estimate of the effective population size was 87 (range: 77–100), i.e. somewhat increased relative to the Norwegian population alone.

Discussion

Figure 1 indicates that the number of animals in the Norwegian Fjord horse population decreased rapidly after the Second World War. Due to a large production of horses during the war on demand from the occupants, the horse population became young, suppressing the production of foals in the first decade after the war (Nestaas, 2010). In addition, thousands of horses were exported to amongst other Poland, Germany, Denmark and Sweden (Dahle, 2006) as an effort to rebuild their infrastructure. These exports also founded the existing populations of Fjord horses in these countries. Contemporary, the mechanization of the farm gradually removed the need for the horse as working power. In Norway, the number of registered horses is relatively complete from 1990, onwards. This is due to a shift from only recording individuals qualified through horse shows to accept all born individuals for the studbook (Seterlund et al., 1989). This peaked the number of horses in 1990, but later the number of registered horses has again drastically decreased, probably due to competition from the imported, specialized sports breeds. Currently, the number of foals born is far below the recommended number of 200 foals per year that is needed at the national ground for sustainable management of the breed (Olsen & Klemetsdal, 2010).

Table 3. Intercept (β_0) and slope ($\beta1$) of $\ln(1-Y)_i = y_i = \beta_0 + \beta_1 \cdot \ln(1-X)_i + e_i$, where X is the kinship coefficient from genomic segments ($f_{seg} \geq 100$ kb) and X is the corresponding coefficient from pedigree (f_{ped}), in the Norwegian (NOR) and the Swedish (SWE) populations. The coefficient of determination (R^2) of the regression model is also included.

		β_0		β_1		R^2	
Y	X	NOR	SWE	NOR	SWE	NOR	SWE
f_{seg}	f_{ped}	−0.068	−0.062	0.983	0.952	0.636	0.819

Despite the reduced population size, the rate of inbreeding in the Norwegian fjord horse population has become strongly moderated the recent decades (Figure 1). This is partly explained by the eight Danish stallions imported and approved for breeding in Norway in the period 1980–2006 (Tor Nestaas, pers. comm.), of which five have had an impact through a considerable amount of progeny, of size 200. The interest for the Danish Fjord horses grew along with the evolvement of the national championship for Fjord horses, started in 1986. The Danish Fjord horses are known to be lighter and, for some enthusiasts, more preferred for use in sports activities. Even though the Danish imports have their origin in Norway, the Norwegian registration rules require only five generations known pedigree for the imports, which may conceal the full relationship to the Norwegian population. In addition, the lack of coordination between stud books in different countries results in a potential underestimation of the level of inbreeding. Still, the pedigrees of the animals in both reference populations were quite complete, with complete generation equivalents of 12.6 in the Norwegian, and 11.5 in the Swedish population, respectively. This is even more complete than what was found in the Døle horse (10.5) and considerably larger than in the Nordland/Lyngen horse (7.2) (Olsen et al., 2010), which are comparable Norwegian horse breeds. Moreover, the values are almost double of what has been found by others (e.g. Rodriguez-Ramilo et al., 2015; Gómez-Romano et al., 2016).

With the possibility of missing genealogical data, as with the Danish imports to Norway, the use of genomic data might lead to improved inference on aspects of

Table 2. Average and range of the inbreeding coefficient based on pedigree (F_{ped}), and of coancestry coefficients from pedigree (f_{ped}) and shared genomic segments ($f_{seg;} \geq 100$ kb) in the Norwegian (NOR) and the Swedish (SWE) populations.

	Mean			Range		
	NOR	SWE	NORxSWE	NOR	SWE	NORxSWE
F_{ped}	0.077	0.052	—[a]	0.005–0.191	0.0008–0.129	—[a]
f_{ped}	0.082	0.065	—[a]	0.030–0.344	0.017–0.311	—[a]
f_{seg}	0.141	0.119	0.115	0.060–0.439	0.055–0.379	0.047–0.396

[a]Not calculated because a unique identity does not exist across the populations in Norway and Sweden.

Table 4. Regression coefficients with belonging standard errors (s.e.) from the regression: $y_i = b_0 + b_1 X_i + e_i$, where y_i is either $1 - F_{ped}$ (F_{ped} being individual inbreeding coefficient from pedigree), or $1 - f_{seg}$ (f_{seg} being coancestry coefficient from shared genomic segments (≥ 100 kb) for animals born ≤ 10 years apart), and X_i denotes the individual birth year (average birth year of the pair), in the Norwegian (NOR), the Swedish (SWE), and in the joint population (All). Also, the calculated effective population size $N_e = 1/2(\Delta F = 1 - e^{b_1})$ with a corresponding confidence interval from $\Delta F = 1 - e^{b_1 \pm 1.96 s.e.}$ for the Norwegian (NOR), the Swedish (SWE), and the joint population (All).

	$b_1 \pm$ s.e.			N_e (confidence interval)		
	NOR	SWE	All	NOR	SWE	All
F_{ped}	$-7.7 \cdot 10^{-4} \pm 5.3 \cdot 10^{-6}$	$-1.6 \cdot 10^{-4} \pm 3.1 \cdot 10^{-6}$	$-^a$	71 (70–72)	269 (259–279)	$-^b$
f_{seg}	$-8.7 \cdot 10^{-4} \pm 5.0 \cdot 10^{-5}$	$-0.4 \cdot 10^{-4} \pm 1.7 \cdot 10^{-4}$	$-5.6 \cdot 10^{-4} \pm 4.0 \cdot 10^{-5}$	63 (57–72)	1136 (119 − ∞)	87 (77–100)

[a]Calculated from a complete pedigree traced back to the founders from the 311 Norwegian and the 102 Swedish horses with a complete generation equivalent of 12.7 and 11.6, respectively, using the software EVA (Berg et al., 2006).
[b]Not calculated because a unique identity does not exist across the populations in Norway and Sweden.

genetic diversity within and between the populations. Here, coancestry of shared genomic segments was used to estimate the average additive relationship between the two genotyped populations, as two times the average coancestry of pairs. Moreover, the coancestry equals the inbreeding coefficient in the offspring of the genotyped animals, for which the rates of change of heterozygosity and the effective population sizes were estimated in the two populations. According to Broman & Weber (1999), a population can be characterized based on the length of their shared segments, with longer segments from more recent ancestors since recombination not yet has had the opportunity to reduce their length. Here, segment lengths as short as 100 kb oriented the change of heterozygosity from genomic coancestry to approximately equal the change of heterozygosity from pedigree. This segment length is very short indicating that much of the inbreeding in these populations are ancient. Therefore, the level of inbreeding from coancestry could become much larger than that from pedigree, despite the considerable pedigree depth that exists in these data.

The close correspondence that exists between coancestry values from genomic and pedigree data is also obvious from Table 3, in both populations. Moreover, the average coancestry values between Norwegian and Swedish horses were close to those found on average within the Norwegian or the Swedish populations. Thus, a considerable additive genetic relationship exists between the two populations, a prerequisite for the development of future joint genetic evaluation across populations. Such a development should be based on genomic relationship rather than on pedigree because a unique identity does not exist across the populations (as between Norway and Sweden). It is likely that all the subpopulations are closely related, albeit it remains to explore the genetic relationship in line with what was done for the Norwegian and Swedish populations herein.

In the Norwegian population, the estimated effective population size from genomic coancestry was lower (63) than the corresponding estimate based on pedigree inbreeding (71). However, in the Swedish population, both estimates were considerably higher, 269 from pedigree inbreeding and 1136 from genomic coancestry, in harmony with the high fraction of immigration. An assumption for the coancestry estimates is random mating. If breeders to some degree are avoiding inbreeding, as for example has been shown in Nordland/Lyngen (Olsen et al, 2010), the genomic coancestry estimates can be considered minimum estimates. On the contrary, the estimate obtained from pedigree inbreeding is corrected for the mating strategy, but not for the missing genealogical data. The difference between the two estimates in the Norwegian population was small (63 vs. 71), meaning that the effect of missingness was only minor. Others that have estimated effective population size for SNP for Norwegian Fjord is Petersen et al. (2013), reporting an estimate of 335 based on a sample of only 21 horses.

The precision of the pedigree estimate of the effective population size was high in both populations as measured by the confidence interval, ranging 70–72 in Norway and 259–279 in Sweden. This was due to including the complete traced pedigree in estimation; 12.7 and 11.6 animals in Norway and Sweden, respectively (Table 4). Using genomic coancestry, the precision was also high in Norway (57–72 effective animals), while it was very imprecisely estimated in Sweden (119–∞). In the genomic estimation, a considerable number of records was utilized, 20,865 pairs in Norway and 2,242 in Sweden (pairs born ≤ 10 years apart) from the 311 and 102 genotyped animals, respectively. So, even though the number of genotyped animals in Sweden was about 1/3 of that in Norway, the fraction of coancestry element became less than 1/9, explaining the much more imprecise estimates in the Swedish population. In fact, it is this huge number of coancestry elements that is the big asset of this method, and it remains to explore what could be gained from utilizing all the possible elements (48,205 and 5151 in the Norwegian and Swedish populations, respectively).

When considering the coancestry from shared segments in both populations, the effective population size increases to 87 (77–100) (Table 4), utilizing 13867 pairs. This indicates that combining the two populations adds genetic variation, which is an important result. Other Fjord horse populations probably possess additional genetic variation, for example, the population of Fjord horses in North-America that has a Norwegian origin (Bhatnagar et al., 2011). Uniting the global population of the Fjord horse is a unique possibility to manage the genetic resources in a sustainable way for the future, and the use of genetic markers will be a powerful tool to both gain knowledge both about the relationship between the subpopulations, serving a basis for joint genetic evaluation, as mentioned, but also in management of the entire genetic variation across the subpopulations. At the same time, such a process represents a considerable political challenge, since there is currently no joint agreement of a common breeding goal for the international Fjord horse.

Across the two examined populations, the effective population size was within the recommended size of 50–100 (Meuwissen & Woolliams, 1994), but with respect to the steadily reduced population size, it seems reasonable to recommend a future effective population size in a long-term perspective closer to or above 100, as suggested by Klemetsdal (1999). To avoid loss of genetic variation in a global population in the future, when performing selective breeding based on a common breeding goal, it will be important to regulate the choice and the use of selection candidates through tools like optimal contribution selection (Sonesson & Meuwissen, 2001).

Conclusion

Utilizing the Norwegian and Swedish Fjord horse population and a relatively small number of genotyped individuals in each country (between 100 and 300), it is shown that coancestry from shared genomic segments can be used to estimate additive genetic relationship and genetic variation within and between the global populations of the Fjord horse. In addition to genetic management purposes, genetic markers are considered a prerequisite for genetic evaluation across these populations, and thus a core in the future development of the breeding of the Fjord horse.

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Disclosure statement

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